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Review

Low Accumulation of Potentially Toxic Elements in Crops: An Integrated Soil–Plant Framework for Food Safety

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Abstract

Contamination of agricultural soils by potentially toxic elements (PTEs) poses a persistent challenge to sustainable crop production and food safety. Because complete remediation of contaminated farmland is often difficult to achieve in the short term, the development and utilization of crop varieties with low PTE accumulation in edible tissues provide a practical strategy for reducing dietary exposure while maintaining agricultural productivity. However, low-accumulation traits arise from coordinated regulation across the soil–plant continuum rather than from a single uptake or detoxification process. This review integrates the major mechanisms governing PTE accumulation in food crops and proposes a regulatory framework encompassing "entry restriction–transport modulation–spatial allocation–cellular immobilization." We first examine how soil physicochemical properties, nutrient–metal interactions, rhizosphere processes, and root structural traits regulate PTE bioavailability and root entry. We then discuss how transporter networks, metal chelation systems, xylem loading, and phloem redistribution control long-distance transport and delivery to aerial and edible organs. Tissue partitioning, cell wall immobilization, and vacuolar sequestration are further considered as key processes determining the final distribution of PTEs within crops. Importantly, similar low-accumulation phenotypes may arise through different regulatory routes, with the relative importance of individual control points varying among elements, crop genotypes, and environmental conditions. These regulatory routes are further discussed in the context of element specificity, strength of supporting evidence, potential trade-offs with mineral nutrition and crop productivity, field robustness, and food-safety relevance. Representative low-accumulation germplasm and current approaches for molecular breeding and agronomic management are also summarized. Together, these considerations position low PTE accumulation as an integrated crop phenotype resulting from multiple, potentially compensatory regulatory processes rather than simply reduced root uptake. Integrating mechanistic understanding with genotype selection and soil–crop management may facilitate the development of low-accumulation crops that combine reduced contaminant delivery to edible tissues with stable agronomic performance, thereby supporting safer and more sustainable production on contaminated agricultural land.

Keywords: low-accumulation crops; soil–plant continuum; rhizosphere processes; element transport; food safety; potentially toxic elements (PTEs)

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1. Introduction

Contamination of agricultural soils by potentially toxic elements (PTEs) has become an important challenge to sustainable crop production and food safety. Unlike many organic contaminants, PTEs are not readily degraded and may persist in soils for long periods, allowing their transfer from soil to crops and subsequently into the human diet [1–3].

Anthropogenic activities, including mining and smelting, industrial emissions, fossil-fuel combustion, and the long-term application of fertilizers and pesticides, have contributed substantially to the accumulation of PTEs in agricultural soils [4,5]. Currently, there are approximately five million contaminated sites worldwide, affecting nearly 500 million hectares of land, with soil heavy metal concentrations in many regions exceeding natural background levels or relevant environmental quality standards [6].

Agricultural soils therefore function not only as sinks for PTEs but also as important sources of dietary exposure when these elements are taken up by crops and accumulate in edible tissues [7–10]. Chronic exposure to toxic elements can cause substantial health effects; for example, Cd exposure is associated with renal dysfunction, whereas Pb can adversely affect neurological and hematopoietic systems [11–13]. The accumulation of PTEs in intensively managed agricultural systems, including some greenhouse soils, further highlights the need to control their transfer from soil to edible crop organs [14].

Consequently, reducing the accumulation of PTEs in edible crop tissues has become an important objective for both the safe utilization of contaminated agricultural land and the production of safer food [15,16]. However, because complete remediation of contaminated farmland is often technically difficult, costly, or slow, complementary strategies that directly limit contaminant accumulation in harvested crop products are increasingly important.

The challenge of controlling PTE accumulation is further complicated by differences in the physiological roles and transport behavior of individual elements. Based on their physiological functions, plant-associated metal elements can be classified into essential and non-essential metals.

The challenge of controlling PTE accumulation is further complicated by differencesin the physiological roles and transport behavior of individual elements. Based on theirphysiological functions, plant-associated metal elements can be classified into essential andnon-essential metals. Plant-associated elements differ substantially in their physiologicalroles and toxicological significance. Fe, Zn, Cu, Mn, and Ni are essential trace elementsrequired for normal plant growth and metabolism, including photosynthesis, respiration, enzyme activity, and redox homeostasis [17–19]. At nutritionally adequate concentrations, these elements support normal physiological functions; however, excessive accumulationcan exceed plant tolerance and cause adverse biological effects [17–19]. By contrast, Cd, Pb, Hg, and As are treated in this review as the principal non-essential PTEs of food-safetyconcern because plants have no established nutritional requirement for them, and theiraccumulation may adversely affect crop performance and human health [20–22].

In the present review, these essential elements are therefore discussed only when excessive accumulation is relevant to toxicity or when their uptake and transport pathways overlap with those of non-essential PTEs and thereby influence contaminant accumulation or nutrient trade-offs. This distinction is particularly important because transport systems involved in the acquisition and redistribution of essential mineral nutrients can also mediate the uptake or movement of non-essential PTEs. For example, Cd uptake and redistribution can involve transport systems that also participate in Mn, Fe, or Zn homeostasis [21,23]. Consequently, strategies aimed at reducing toxic-element accumulation must be evaluated not only for their effects on contaminant concentrations but also for their potential impacts on essential mineral nutrition, crop growth, and yield.

This functional overlap creates a fundamental challenge for low-accumulation crop improvement: reducing the entry and transfer of toxic elements without compromising essential mineral nutrition, crop growth, or yield. Thus, low-accumulation traits should be evaluated not only in terms of contaminant reduction but also in relation to their potential nutritional and agronomic trade-offs.

From a food-safety perspective, the significance of crop PTE accumulation extends beyond plant toxicity itself. Because PTEs can enter the human diet through crop consumption, regulatory authorities have established commodity-specific maximum levels for contaminants such as Cd, Pb, As, and Hg in cereals, vegetables, fruits, and other food products [20,24–26]. These regulatory limits provide an important basis for evaluating food compliance and for managing contaminated agricultural land. However, permissible concentrations vary among elements, food commodities, jurisdictions, and regulatory systems and should therefore be interpreted within their specific regulatory context.

Importantly, compliance with a concentration-based regulatory limit and actual dietary exposure are related but not equivalent measures of food safety. Human exposure depends not only on contaminant concentration in edible tissues but also on food consumption rate, exposure frequency, body weight, and population-specific dietary patterns. Consequently, exposure-based indicators such as estimated daily intake (EDI), hazard quotient (HQ), hazard index (HI), and, where appropriate, carcinogenic risk can provide complementary information when evaluating the food-safety significance of low-accumulation crops.

In contaminated farmland, crops may maintain apparently normal growth and yield while still accumulating PTEs in edible organs at concentrations that compromise food compliance or contribute to chronic dietary exposure [20,27]. Because complete soil remediation is not always immediately feasible, reducing the transfer of PTEs into harvested tissues represents a practical complementary strategy for safe agricultural production.

Against this background, low-accumulation crops have attracted increasing attention as a complementary strategy for reducing contaminant transfer into harvested products. Low-accumulation crops generally refer to crop species or genotypes that maintain comparatively low concentrations of a target PTE in edible tissues under comparable exposure conditions [20]. Substantial interspecific and genotypic variation has been documented among food crops. In rice, for example, variation in transport-related genes can markedly alter grain Cd accumulation, and low-Cd germplasm has been incorporated into breeding programs [23,28,29]. Low-Cd, high-yield germplasm has also been identified in other crops, indicating that contaminant reduction can, in some cases, be combined with agronomic performance [30]. PTE accumulation also differs among crop types and edible organs [31,32], and targeted genetic manipulation can further modify contaminant accumulation [33]. These findings indicate that low accumulation can arise through multiple physiological and genetic mechanisms rather than through a single universal pathway [34].

A central question is therefore why crop species or genotypes exposed to comparable contamination conditions can nevertheless differ markedly in PTE concentrations in their edible organs. Reduced root uptake represents only one possible explanation. Low edible-tissue accumulation may also result from restricted xylem loading or phloem redistribution, preferential retention in roots or vegetative tissues, altered organ-specific allocation, enhanced cell-wall binding, or vacuolar sequestration. Conversely, relatively low root uptake does not necessarily ensure low accumulation in edible organs if the absorbed fraction is efficiently transported toward reproductive or other harvested sinks. Thus, low root uptake and low edible-tissue accumulation should not be regarded as equivalent traits.

Previous reviews have provided important syntheses of PTE uptake and transport, detoxification, phytoremediation, crop improvement, and food-safety-related strategies [16,20,21,25,27,34]. Some have also traced Cd accumulation from the rhizosphere to

edible crop tissues. However, a remaining analytical challenge is to explain how mechanistically distinct control points across the soil–plant continuum can converge on similar low-accumulation phenotypes, and how these control points differ in their evidential support and translational relevance. To clarify how the present framework differs from previous syntheses, representative reviews are compared according to their principal focus, regulatory levels covered, relevance to edible tissues, and major scope boundaries (Table 1).

Accordingly, this review addresses three related questions: (i) Which experimentally supported control points can reduce PTE delivery to edible tissues in food crops? (ii) How do the type and strength of evidence differ among these control processes and across the major PTEs considered? (iii) Which mechanisms currently have sufficient agronomic, nutritional, and field support to represent promising targets for crop improvement or management? To address these questions, we organize the available evidence within four functionally distinct but interconnected regulatory processes: entry restriction, transport modulation, spatial allocation, and cellular immobilization.

Rather than treating these processes as a strictly sequential pathway, the review evaluates whether alternative and potentially compensatory regulatory routes can generate similar low-accumulation phenotypes. Particular attention is given to element specificity, evidence strength, effects on essential mineral nutrition and crop productivity, field robustness, and food-safety relevance. Because the available evidence is unevenly distributed among PTEs and crop groups, with Cd and rice being particularly well represented, the framework is not intended to imply equivalent mechanistic support across all crop–element combinations. Instead, it provides a common basis for identifying where evidence is strong, limited, or still lacking and for linking mechanistic understanding with the development and deployment of low-accumulation crops.

Table 1. Comparison of representative reviews addressing PTE accumulation in crops and the scope of the present review.

Representative Review	Main Focus	Major Regulatory Levels Covered	Food Crop/Edible-Tissue Relevance	Strengths and Scope Boundaries	Added Value of the Present Review
Page & Feller, 2015 [35]	Whole-plant transport and redistribution of metals	Root uptake, xylem loading, long-distance transport, phloem redistribution	Moderate	Provides a clear framework for whole-plant metal transport and redistribution; rhizosphere regulation, cellular immobilization, and low-accumulation crop development are not its principal focus	Extends transport-centered concepts to entry restriction, tissue allocation, cellular immobilization, and final accumulation in edible organs
Clemens & Ma, 2016 [27]	Toxic metal/metalloid accumulation in crops and food	Uptake, translocation, speciation, transporters, natural variation	Strong	Provides strong mechanistic and food-safety perspectives, particularly for As and Cd; it predates much of the recent evidence on low-accumulation germplasm, breeding, and field validation	Integrates more recent evidence with rhizosphere processes, tissue/cellular regulation, agronomic trade-offs, and field applicability
Clemens, 2019 [25]	Reducing toxic-element accumulation in crops for safer food	Molecular uptake and transport mechanisms, crop improvement, food-safety implications	Strong	Directly connects plant science with safer food, but does not organize low-accumulation phenotypes according to alternative regulatory control points across the complete soil–plant continuum	Examines how different regulatory routes can converge on similar low-accumulation phenotypes in edible tissues
Elango et al., 2022 [16]	Agronomic, breeding, and biotechnological mitigation of heavy-metal toxicity	Agronomic management, phytoremediation, breeding, biotechnology	Moderate	Broadly addresses agricultural mitigation and crop tolerance; low accumulation in edible tissues is not the central organizing concept	Links mitigation strategies to defined mechanisms controlling contaminant delivery to edible organs
Lin et al., 2024 [34]	Low-Cd accumulation in crops from rhizosphere soil to edible parts	Rhizosphere, root uptake, transport, chelation, detoxification, cultivar differences	Strong	The closest existing framework to the present review, but specifically centered on Cd and with less emphasis on cross-element differences, evidence hierarchy, nutrient/yield trade-offs, and field validation	Extends the low-accumulation framework across multiple PTEs and explicitly evaluates element specificity, evidence strength, agronomic trade-offs, field relevance, and food-safety implications

Table 1. *Cont.*

Representative Review	Main Focus	Major Regulatory Levels Covered	Food Crop/Edible-Tissue Relevance	Strengths and Scope Boundaries	Added Value of the Present Review
Huang et al., 2024 [21]	Metal transport systems in plants	Uptake, translocation, distribution, redistribution, transporter regulation	Moderate to strong	Provides a detailed mechanistic synthesis of metal transporters and includes safer crop production; rhizosphere processes, field management, and non-transporter determinants are not its main focus	Places transporter regulation within a broader phenotype-oriented framework including rhizosphere, tissue allocation, cellular sequestration, and agronomic context
Present review	Formation of low-accumulation phenotypes in food crops across the soil–plant continuum	Entry restriction, transport modulation, spatial allocation, cellular immobilization, breeding and management	Central focus	Provides a cross-scale synthesis centered on edible tissues and translational relevance. Evidence remains uneven among PTEs and crop groups, with Cd and major cereal crops disproportionately represented, and study heterogeneity limits quantitative attribution of individual regulatory processes.	Integrates alternative mechanistic routes leading to low accumulation and evaluates them in relation to element specificity, evidence strength, nutrient/yield trade-offs, field validation, and food-safety relevance.

Note: Reviews included in this table were selected from the literature identified through the search process described in Section 2, last updated on 19 October 2026, and are presented as representative rather than exhaustive examples. Reviews were considered for comparison when they addressed multiple stages of the soil–plant continuum; focused on PTE uptake, transport, sequestration, low-accumulation traits, or food-crop safety; and provided a conceptual basis relevant to the questions addressed in the present review. Comparisons are based on the principal scope and analytical emphasis of each review. "Scope boundaries" refer to topics that were not the primary focus of the respective reviews and should not be interpreted as methodological shortcomings. The present review adopts a phenotype-oriented perspective centered on PTE accumulation in edible tissues and integrates entry restriction, transport modulation, spatial allocation, and cellular immobilization with element specificity, evidence strength, agronomic trade-offs, field robustness, and food-safety relevance. Abbreviations: PTEs, potentially toxic elements; Cd, cadmium; Pb, lead; As, arsenic; Hg, mercury.

2. Literature Search, Study Selection, and Evidence Classification

This review was conducted as a structured narrative synthesis. Literature was identified primarily through the Web of Science Core Collection, with the principal search covering studies published from 1 January 2014 to 19 October 2026. Eight complementary thematic search sets were used to identify studies addressing low-accumulation phenotypes and genotypic variation, entry restriction, internal transport and redistribution, spatial allocation, cellular immobilization, phenotype and field validation, rhizosphere and soil-management processes, and subcellular partitioning. Because Cd represents the most extensively studied PTE in low-accumulation crops, the principal thematic searches were centered on Cd, while evidence for Pb, As, Hg, and essential trace elements was incorporated where relevant to cross-element comparison, shared transport pathways, nutrient interactions, and food-safety implications. The complete search terms, Boolean combinations, search date, and numbers of records retrieved for each thematic search are provided in Supplementary Table S1.

Studies were prioritized when they investigated food or horticultural crops with edible organs relevant to human dietary exposure and provided physiological, molecular, genetic, agronomic, or field evidence related to at least one of the four regulatory processes considered here: entry restriction, transport modulation, spatial allocation, and cellular immobilization. Studies focusing exclusively on non-food hyperaccumulators, phytoremediation species, or environmental matrices without crop-related outcomes were not included in the primary crop-focused synthesis. Review articles were used primarily for conceptual context and comparison with previous syntheses. Earlier studies published before 2014 were retained selectively when they provided foundational evidence for established uptake, transport, metal-speciation, or sequestration mechanisms.

Evidence was interpreted according to the nature of the supporting observations. Associative evidence was distinguished from experimental interventions and from genetic or functional validation, while field evidence was considered separately when low-accumulation phenotypes were demonstrated under agricultural conditions. Particular attention was given to the target element, crop genotype, experimental conditions, measured tissue, effects on edible-organ PTE accumulation, and, where available, effects on yield and essential mineral composition. Reductions in root or shoot PTE concentrations were not considered equivalent to reductions in harvested edible organs. Because of substantial heterogeneity among crop species, elements, experimental systems, exposure conditions, and reported outcomes, no formal meta-analysis was performed.

3. An Integrated Regulatory Framework for Low-Accumulation Phenotypes Along the Soil–Plant Continuum

3.1. Three Regulatory Levels Encompassing Four Major Control Processes

The concentration of potentially toxic elements (PTEs) in edible crop tissues is the cumulative outcome of multiple transfer and retention processes operating along the soil–plant continuum rather than the consequence of a single uptake or detoxification mechanism [36–38]. From soil exposure to final accumulation in harvested organs, four major control processes can be distinguished: entry restriction, transport modulation, spatial allocation, and cellular immobilization. These processes operate across three interconnected regulatory levels (Figure 1).

The first regulatory level operates at the soil–rhizosphere–root interface and primarily determines the amount of PTEs entering the plant. Soil physicochemical properties, element speciation, rhizosphere processes, root architecture, apoplastic barriers, and membrane transport systems collectively regulate PTE bioavailability and root entry [39–41]. This

level therefore determines the initial input of PTEs into the plant system and corresponds primarily to entry restriction.

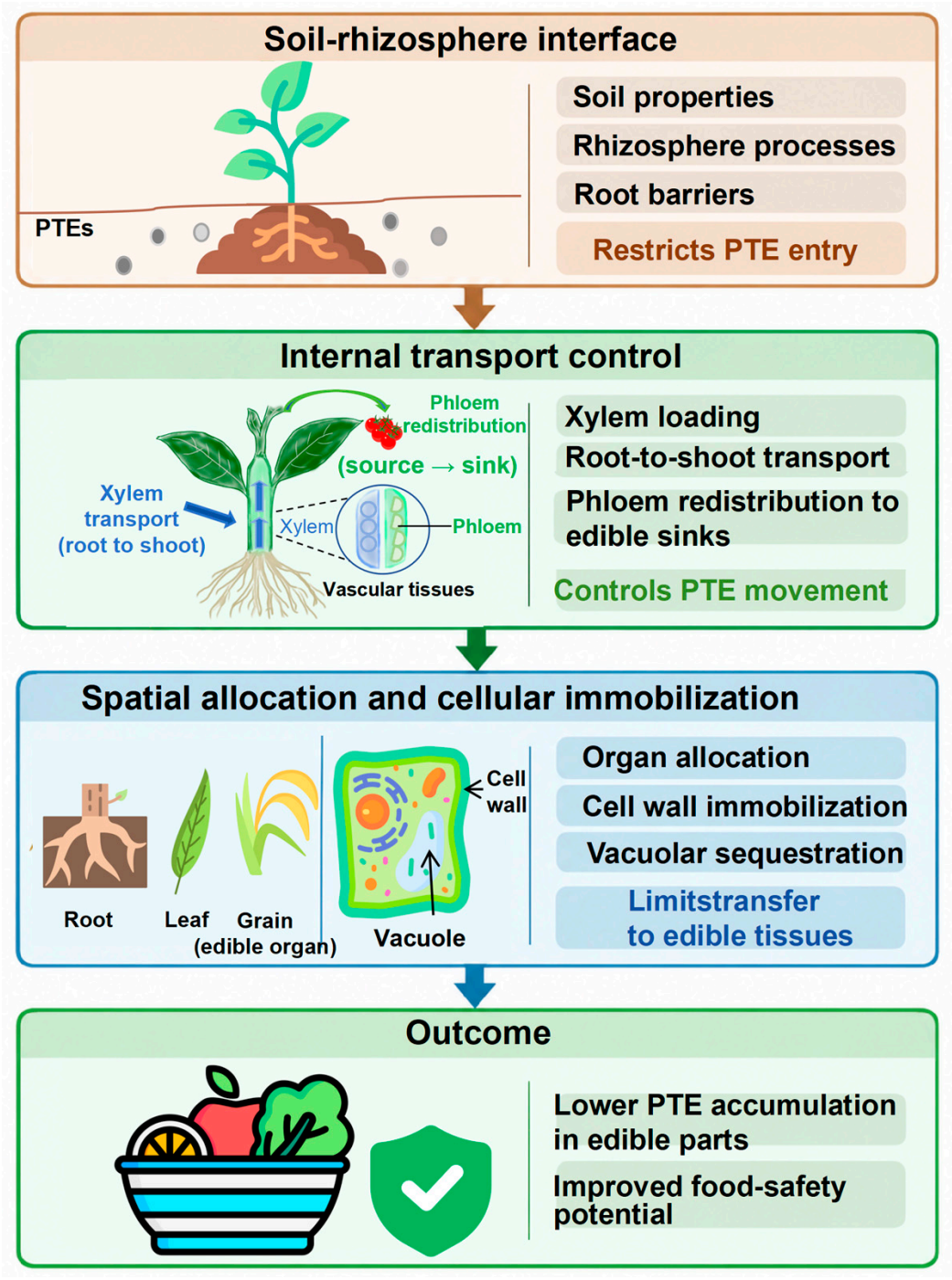


Figure 1. Integrated regulatory framework for the formation of low-accumulation phenotypes along the soil–plant continuum. Four major control processes—entry restriction, transport modulation, spatial allocation, and cellular immobilization—operate across three interconnected regulatory levels.

The second regulatory level operates during internal transport and controls the movement of absorbed PTEs among roots, stems, leaves, and reproductive or edible organs. Processes including xylem loading and unloading, long-distance transport, phloem redistribution, chelation, and transporter-mediated transfer determine the efficiency with which PTEs are delivered to aboveground and edible tissues [42,43]. This level corresponds mainly to transport modulation.

The third regulatory level operates at the tissue and cellular scales. At the tissue level, preferential retention in roots, stems, leaves, or other non-edible organs can reduce transfer toward harvested tissues, representing spatial allocation. At the cellular level, cell-wall binding, chelation, and vacuolar sequestration can further reduce the mobility and redistribution of PTEs, representing cellular immobilization [42,44,45].

Thus, the proposed framework comprises three regulatory levels but four functionally distinct control processes. Their combined effects determine the efficiency of PTE transfer from soil to edible crop tissues and ultimately shape the low-accumulation phenotype.

3.2. Alternative Regulatory Routes and Interactions Among Control Processes

The four regulatory processes proposed here should not be regarded as a strictly sequential pathway in which low accumulation requires simultaneous restriction at every step. Instead, mechanistically distinct control routes may converge on a similar low-accumulation phenotype in edible tissues. In some crop genotypes, reduced PTE entry at the soil–root interface may represent the dominant control point, whereas in others substantial root uptake may occur but subsequent xylem loading, phloem redistribution, or allocation to edible organs is strongly restricted. Preferential retention in roots or vegetative tissues and enhanced cellular immobilization may provide additional routes by which PTE delivery to harvested organs is reduced [27,34].

The central conceptual proposition of this framework is therefore that low root uptake and low edible-tissue accumulation are not equivalent traits, and that similar low-accumulation phenotypes may arise from different dominant control points. The relative contribution of these control processes is expected to vary with element chemistry, crop genotype, environmental conditions, and agronomic management. Accordingly, the framework is intended to identify the dominant control point, or combination of control points, operating within a particular crop–element–environment system rather than to define a universal mechanism of low accumulation.

3.3. From a Conceptual Framework to Measurable Control Points

Each regulatory process can be linked to measurable variables that allow its relative contribution to low accumulation to be evaluated. Entry restriction can be assessed using soil-bioavailable PTE fractions, root accumulation, and uptake coefficients. Transport modulation can be evaluated using root-to-shoot translocation, xylem and phloem PTE concentrations, and transporter activity. Spatial allocation can be characterized through organ-specific distribution patterns and tissue partitioning, whereas cellular immobilization can be assessed by quantifying cell-wall-associated, chelated, or vacuolar PTE fractions.

These mechanistic variables should ultimately be related to PTE concentrations in harvested edible tissues together with agronomic outcomes such as yield and essential mineral composition. The framework therefore generates two testable predictions. First, crop genotypes with similarly low PTE concentrations in edible organs may differ in the regulatory process that contributes most strongly to that phenotype. Second, measurements of root uptake alone should not consistently predict edible-tissue accumulation when transport modulation, spatial allocation, or cellular immobilization represents the dominant control point. Testing these predictions across contrasting genotypes, elements, and environments may provide a more mechanistically informative basis for breeding and management than evaluation of total plant uptake alone.

4. Regulation of PTE Entry at the Soil–Rhizosphere–Root Interface

The entry of potentially toxic elements (PTEs) into crops is initiated by a series of processes operating across the soil–rhizosphere–root interface. As a critical boundary link-

ing the soil environment and plant roots, this interface determines both the bioavailability of PTEs and the initial flux of metal uptake into plants [46]. Importantly, the efficiency of this first regulatory step is strongly element-dependent because PTEs differ in chemical speciation, charge, redox sensitivity, and interactions with soil minerals and plant nutrient-acquisition pathways.

4.1. Soil Physicochemical Controls on PTE Bioavailability

Soil physicochemical properties represent the primary determinants of PTE bioavailability, among which soil pH is considered one of the most influential factors governing metal mobility and plant uptake efficiency [47,48]. For many cationic metals, including Cd, Pb, and Zn, acidic conditions generally increase the proportion of soluble and exchangeable forms, thereby increasing their potential availability for plant uptake. In contrast, under neutral or alkaline conditions, these metals tend to form precipitates or stable complexes with carbonates, phosphates, or organic ligands, thereby reducing their bioavailability [49–51]. Accordingly, increasing soil pH can be an effective strategy for reducing the mobility of many cationic PTEs, although this relationship should not be generalized to all elements. For example, the application of mineral amendments such as processed oyster shell powder and attapulgite can reduce Cd availability in acidic paddy soils and consequently decrease Cd accumulation in rice grains [52].

In contrast, the environmental behavior of metalloids such as As is governed more strongly by chemical speciation, redox potential (Eh), Fe mineral dynamics, and interactions with competing oxyanions. Changes in pH or redox conditions may therefore influence As availability differently from that of cationic metals such as Cd. Consequently, a soil-management practice that effectively immobilizes one PTE does not necessarily exert the same effect on another [20,27].

In addition to soil pH, soil organic matter content is another key factor regulating heavy metal speciation and mobility. Organic matter can immobilize metal ions through adsorption, complexation, and precipitation processes, thereby reducing the fraction of bioavailable metal species [53]. Based on this principle, soil amendments can alter Cd bioavailability through changes in soil physicochemical conditions and rhizosphere microbial processes, thereby influencing Cd transfer to vegetable crops [54–56]. For instance, husk-biochar amendment altered soil Cd availability and reduced Cd accumulation in pak choi grown in contaminated soil, illustrating how organic amendments can restrict plant exposure to bioavailable Cd [57]. However, the effects of organic matter are also element- and amendment-dependent because dissolved organic ligands may alter metal complexation and mobility rather than invariably promoting immobilization.

Furthermore, competition between essential nutrients and PTEs represents another important mechanism regulating plant uptake. Essential elements such as Ca, Fe, Mn, and Zn can compete with toxic metals like Cd for adsorption sites in the rhizosphere or for transport pathways across root cell membranes, thereby inhibiting their entry into plants [27,58]. For example, silicon fertilization can reduce Cd bioavailability in the rhizosphere through changes in soil chemistry and immobilization processes, significantly decreasing Cd accumulation in multiple crop species [58]. Similarly, Xin et al. (2023) reported that boron application can modulate Cd uptake and shoot translocation in pepper through antagonistic interactions, indicating that nutrient management not only optimizes plant nutritional status but also effectively regulates heavy metal accumulation via elemental competition and antagonism [59]. These interactions are likewise element-specific; for example, arsenate [As(V)] uptake can be influenced by phosphate availability because As(V) and phosphate share related uptake pathways, whereas Cd uptake is more strongly affected by interactions with cationic nutrients and metal transport systems [27].

Collectively, soil physicochemical conditions regulate the size and chemical form of the PTE pool potentially accessible to roots. However, the direction and magnitude of these effects depend on element chemistry; therefore, soil-based entry restriction should be evaluated separately for different PTEs rather than treated as a universally applicable mechanism.

4.2. Rhizosphere Processes Modulate PTE Availability

As a dynamic interface connecting soil and plants, the rhizosphere plays a pivotal regulatory role in controlling the transfer efficiency of PTEs from soil to plants through tightly coupled chemical and biological processes. Unlike a simple immobilization barrier, the rhizosphere can either decrease or increase PTE availability depending on the element, root exudate composition, microbial community, and surrounding soil conditions.

From a chemical perspective, root exudates—including organic acids, amino acids, phenolic compounds, and polysaccharides—are continuously released by plant roots and act as key modulators of rhizosphere chemistry. These compounds regulate the mobility and bioavailability of PTEs by altering rhizosphere pH and modifying the complexation state of metal ions [60,61]. Accordingly, root exudation should not be interpreted as an exclusively protective process: depending on ligand chemistry and element speciation, exudates may either immobilize PTEs or enhance their solubilization and mobilization.

From a biological perspective, substantial variation in both the composition and quantity of root exudates among crop species and cultivars leads to distinct responses in heavy metal uptake. Root-exudate composition can also influence PTE partitioning within crops. In spring wheat, variation in root-exudate composition was associated with differences in Cd partitioning between roots and shoots [62]. In terms of quantity, a comparative study of 15 amaranth varieties showed that low-Cd-accumulating varieties released lower levels of soluble root exudates in the rhizosphere, which weakened the co-mobilization of Cd with essential elements such as Ca and Zn, ultimately reducing Cd uptake by roots [63]. These studies further indicate that genotypic variation in rhizosphere chemistry can contribute to differences in low-accumulation phenotypes even under comparable soil exposure.

In addition, rhizosphere microorganisms can further modify PTE availability and plant uptake. In lettuce, poly-γ-glutamic-acid-producing bacteria reduced Cd uptake while altering the rhizosphere microbial community [64,65]. Arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) are representative examples, which reduce heavy metal translocation by immobilizing Cd, modifying rhizosphere chemical conditions and enhancing plant stress tolerance [66–68]. Mechanistically, polyamine-producing bacterial strains reduced the bioavailable fractions of Cd and Pb through polyamine-mediated chelation and cell-surface precipitation, resulting in 51–80% lower Cd and Pb contents in water spinach compared with uninoculated controls [69]. However, microbial transformation can also increase the mobility of particular PTE species under some conditions, especially when redox-sensitive elements are involved. Thus, microbial effects on PTE entry are context- and element-dependent rather than uniformly suppressive.

Together, root exudation and microbial processes make the rhizosphere a bidirectional regulator rather than a simple barrier to PTE entry. Whether this interface promotes or restricts uptake depends on the balance between mobilization and immobilization processes and can therefore differ among crop genotypes, elements, and soil environments.

4.3. Root Structural and Morphological Controls on PTE Entry

After PTEs pass through the rhizosphere, the anatomical structures and morphological traits of roots collectively determine their efficiency of entry into plant tissues. These controls operate through two conceptually distinct mechanisms: anatomical barriers restrict

apoplastic transport, whereas root-system architecture influences the effective absorptive interface between roots and soil.

From the perspective of passive barriers, the Casparian strip in the root endodermis serves as the primary checkpoint controlling radial transport of PTEs toward the stele [70,71]. By disrupting apoplastic continuity, this structure forces ions to cross plasma membranes via the symplastic pathway, thereby enhancing selectivity in metal uptake [27,72]. Strengthening of the Casparian strip has therefore been recognized as an effective strategy to restrict heavy metal entry. For example, under boron-sufficient conditions, cadmium stress induces a significant increase in Casparian strip width in pepper roots. This effect is associated with the upregulation of lignin biosynthesis-related genes in endodermal cells, leading to enhanced lignification and reinforced apoplastic barriers, which restricts Cd influx into the stele [17].

In addition to the Casparian strip, modifications of root cell walls constitute another important component of the apoplastic barrier system. The deposition of suberin and lignin in the endodermis and exodermis further strengthens apoplastic restriction, limiting the movement of PTEs such as Cd toward vascular tissues and reducing their long-distance transport to shoots [73,74]. A representative example is nano-selenium treatment, which enhances Cd tolerance by upregulating key lignin biosynthesis genes (e.g., PAL and CAD), increasing lignin precursor accumulation and maintaining cell wall integrity, ultimately reducing Cd accumulation in pepper plants [75].

In contrast to these passive structural barriers, root morphological traits regulate heavy metal uptake through active modulation of absorptive capacity. Generally, increased root length and higher root hair density expand the absorptive surface area, whereas a larger root diameter reduces the surface area per unit biomass; thus, variation in root architecture leads to substantial differences in heavy metal uptake capacity [76]. This relationship has been validated across multiple species. For instance, rice cultivars with smaller root surface areas or fewer root hairs tend to accumulate lower levels of Cd [76]. In pak choi, total Cd accumulation is significantly and positively correlated with root length, surface area, volume, and fine root proportion, with high-accumulating cultivars typically exhibiting more developed root systems [77]. These associations support a contribution of root architecture to PTE accumulation, although correlations between root traits and metal concentration should not by themselves be interpreted as direct causal evidence. Moreover, root architecture exhibits strong plasticity under heavy metal stress. For example, Cu exposure induces reduced specific root length but increased root diameter and branching density in radish, indicating a shift toward a thicker and more highly branched root system [78].

Taken together, root anatomical barriers and root-system architecture influence PTE entry and radial transport within roots, thereby contributing to variation in the amount of PTEs available for subsequent vascular transport. However, restriction at the root-entry stage represents only one possible route toward a low-accumulation phenotype. Reduced root uptake does not necessarily result in low concentrations in edible tissues because PTEs that enter the plant remain subject to xylem loading, long-distance transport, redistribution, and tissue allocation. Root-entry regulation should therefore be regarded as an early control stage in the soil–plant continuum rather than as a sufficient determinant of final PTE accumulation in edible organs.

Soil physicochemical properties regulate PTE speciation and bioavailability, whereas root exudates and rhizosphere microorganisms may promote either mobilization or immobilization depending on element chemistry and environmental conditions. Root anatomical barriers and root-system architecture further regulate PTE entry and radial movement toward the stele.

Soil physicochemical properties regulate PTE speciation and bioavailability, where-asroot exudates and rhizosphere microorganisms may promote either mobilization or immo-bilization depending on element chemistry and environmental conditions. Root anatomicalbarriers and root-system architecture further regulate PTE entry and radial movementtoward the stele (Figure 2).

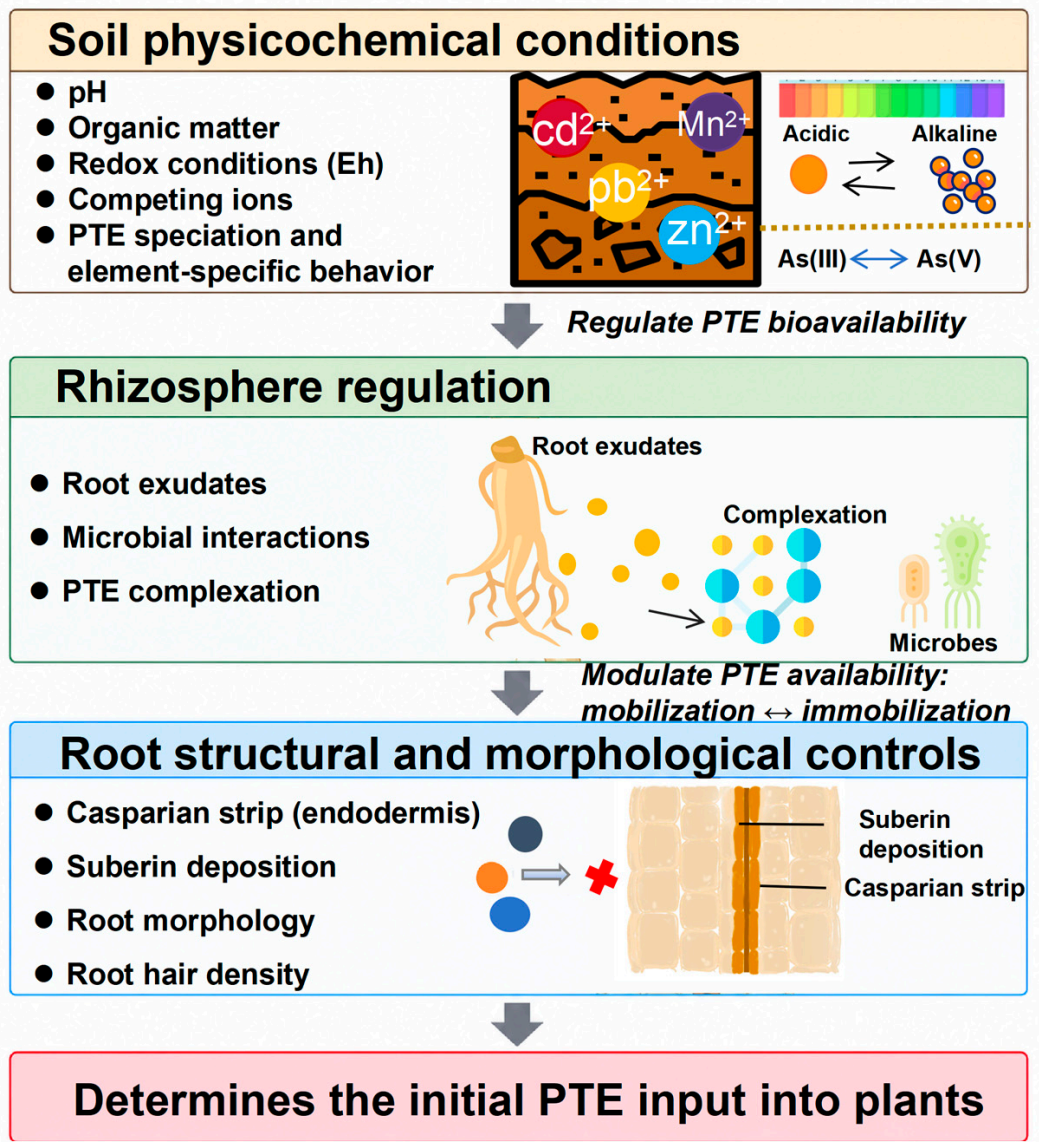


Figure 2. Element-specific regulation of potentially toxic element entry at the soil–rhizosphere–root interface.

5. Regulation of PTE Transport and Redistribution Within Plants

Once PTEs have entered the root system, their accumulation in edible tissues depends not only on the amount absorbed but also on the efficiency and direction of subsequent vascular transport and redistribution. This transport stage therefore represents a second major control point separating root uptake from final accumulation in harvested organs.

5.1. Xylem Loading and Long-Distance Upward Transport

After entering the root system, PTEs can be transported through the plant vascular system, with xylem transport representing a major route for root-to-shoot translocation [79]. In this process, PTEs are first loaded into xylem vessels in the root and subsequently

transported with the transpiration stream from roots to aboveground tissues, including stems and leaves [23,80,81]. The efficiency of xylem loading therefore provides an important regulatory point determining how much of the PTE pool retained in roots becomes available for subsequent transport to aerial organs.

Significant variation exists among crop species and cultivars in xylem transport efficiency. In high-accumulating types, PTEs are efficiently loaded into the xylem and rapidly translocated to shoots via transpiration flow, leading to substantial accumulation in leaves or grains [82]. For example, the high-accumulating rapeseed cultivar L351 exhibits strong Cd translocation to shoots; although its root uptake capacity is relatively low, its xylem transport efficiency is significantly higher than that of low-accumulating cultivars [83]. Similarly, in peanut, high-accumulating cultivars such as Qishan 208 and Xuhua 13 show significantly higher Cd accumulation in shoots. This variation is mainly attributed to differences in Fe transport activity, xylem loading capacity, and transpiration rates, with transpiration rate positively correlated with leaf Cd concentration and translocation factor [84]. These examples illustrate that differences in vascular transfer efficiency can generate contrasting shoot-accumulation phenotypes even when root uptake alone does not differ in the same direction.

In some low-accumulating genotypes, restricted xylem loading and long-distance transport constitute major mechanisms limiting PTE delivery to aboveground tissues [85]. For instance, in pak choi, low-Cd cultivars immobilize more Cd in root cell walls or compartmentalize it into vacuoles, thereby limiting its translocation to shoots [86]. In maize, the low-accumulating genotype L63 exhibits a significantly lower Cd translocation rate than the high-accumulating genotype L42, primarily due to reduced xylem loading capacity, as confirmed by transcriptomic and metabolomic analyses [87].

At the molecular level, xylem loading is mainly regulated by the coordinated action of membrane transporters and metal-chelating ligands, which together determine the efficiency of metal release from root cells into xylem vessels [88,89]. For example, exogenous tryptophan (Trp) treatment reduced Cd accumulation in broccoli shoots by 51.6%, potentially through the suppression of HMA4 expression and the resulting restriction of root-to-shoot Cd transport [90]. In rice, OsHMA2 mediates the transport of Zn and Cd from roots to shoots, and its expression level is closely correlated with shoot metal accumulation, supporting an important role for OsHMA2 in xylem loading and long-distance transport [91].

Furthermore, NRAMP and ZIP transporter families regulate transmembrane metal uptake and intracellular metal partitioning, thereby influencing the metal flux entering the xylem and indirectly determining long-distance transport efficiency [92]. For instance, OsZIP7 facilitates Zn and Cd loading into the xylem in roots and mediates subsequent redistribution between xylem and phloem in nodes, enabling precise delivery to developing grains [93]. In radish, RsNRAMP5 acts as a major transporter promoting Cd influx and plays a key role in root Cd uptake and accumulation [94]. In addition, silicon supplementation reduces Cd concentrations in wheat roots and shoots by 67.45% and 70.34%, respectively, partly through the regulation of metal transporter-related pathways, including ZIP and NRAMP5 [95]. These examples further illustrate that root uptake and xylem loading are mechanistically connected but represent distinct regulatory steps.

At the system level, transcriptomic and functional analyses in pepper (*Capsicum annuum*) demonstrate that multiple transporters act in concert to regulate Cd distribution between roots and shoots, forming a complex regulatory network [96]. Accordingly, xylem transport should be viewed as an integrated outcome of transporter activity, ligand availability, and transpiration-driven mass flow rather than as a single-gene process.

5.2. Element-Specific Mobility and Phloem Redistribution

PTEs and essential trace elements exhibit pronounced differences in their long-distance mobility within plants, and variation in phloem redistribution represents an important determinant of their final distribution in edible tissues. Among the elements examined in previous studies, Ni exhibits relatively high phloem mobility, whereas Zn and Cd show intermediate mobility; Fe and Mn may be more strongly retained in mature or senescent tissues following xylem transport [97,98]. Such differences arise from element-specific transport pathways, ligand-binding properties, chemical speciation, and source–sink dynamics rather than from a single universal mobility pattern.

Comparative studies further support this element-specific behavior. In wheat, bean, and lupine, Cd export to shoots occurs more slowly than that of Zn. In Solanum nigrum, the phloem-mediated redistribution of 65Zn from old leaves to developing tissues such as young leaves, flowers, and fruits is substantially more efficient than that of 109Cd [99], directly demonstrating the differential mobility among elements. These observations caution against extrapolating vascular-transport behavior from one element to another.

These element-dependent transport properties make phloem redistribution an important control point for PTE accumulation in edible organs. During plant development, assimilates are transported through the phloem from source tissues to sink organs such as fruits and seeds; PTEs entering this pathway may therefore be redistributed toward edible tissues [35,100]. The importance of this pathway is particularly evident for reproductive organs, in which final accumulation may depend strongly on post-xylem redistribution rather than on root uptake alone.

Importantly, both essential and non-essential elements can utilize this pathway. For instance, zinc can be remobilized from senescent leaves to developing tissues under deficiency conditions in apple [98]. Conversely, even when root uptake is relatively limited, cadmium can still be transported to fruits via the phloem in fruit crops [101]. A quantitative study by Ouyang et al. further highlights the significance of this pathway, showing that under combined root and foliar Cd exposure, root uptake accounted for up to 90.4% of Cd accumulation in pepper fruits, with both xylem and phloem contributing to Cd transport into fruits [102]. Together, these findings show that the contribution of xylem and phloem pathways to edible-tissue accumulation is crop-, organ-, and element-dependent. Therefore, low root or shoot accumulation cannot be assumed to predict low concentrations in reproductive organs without considering source–sink redistribution.

5.3. Integrated Regulation and Molecular Basis of Transport Processes

Long-distance transport and redistribution of PTEs in plants do not occur as independent processes but are jointly influenced by transporter activity, ligand chemistry, vascular loading and unloading, and source–sink relationships. These processes determine not only the magnitude of PTE movement but also its direction and destination within the plant.

At the transporter level, members of the NRAMP, ZIP, and HMA families play central roles in transmembrane uptake, xylem loading, and redistribution [92,103,104]. For instance, mutation of OsNRAMP5 in rice significantly reduces Cd transport efficiency through multiple coordinated effects, including enhanced Cd retention in root cell wall cellulose and suppression of OsHMA2- and OsCCX2-mediated xylem loading as well as citrate- and tartrate-dependent long-distance transport [105]. In contrast, hydrogen peroxide treatment promotes Cd phloem loading in association with increased OsHMA2 expression, thereby increasing Cd accumulation in rice shoots [106]. Together, these observations illustrate how transporter regulation at different stages of internal transport can alter the direction and efficiency of PTE movement within plants.

At the chelation level, the mobility of PTEs is largely determined by their chemical speciation and ligand stability. Computational analyses have shown that nicotianamine (NA) is the dominant chelator in the phloem, binding nearly all Fe^{2+} but only 20–50% of other micronutrients, indicating strong element-dependent differences in complexation affinity [107]. Further evidence from sweet potato demonstrates that 50–70% of Cd in phloem sap exists in low-molecular-weight complexes, providing direct confirmation that Cd can be transported in chelated forms over long distances [108]. PTEs and essential trace elements exhibit pronounced differences in their long-distance mobility within plants, particularly in their capacity for phloem redistribution.

In addition to nicotianamine, phytochelatins (PCs), metallothioneins (MTs), and organic acids contribute to metal chelation and influence the distribution of potentially toxic elements within plants [109–112]. However, their effects on accumulation in edible organs are highly element- and genotype-dependent. In rice, disruption of OsPCS1 reduced Cd accumulation in grains but increased As accumulation in one mutant background, demonstrating contrasting roles of phytochelatin-dependent pathways in the partitioning of different elements [110]. Similarly, cultivar-dependent differences in phytochelatin metabolism have been associated with variations in Cd accumulation in lettuce [112]. These observations indicate that enhanced chelation does not necessarily lead to lower PTE concentrations in edible tissues; its contribution depends on element identity, tissue localization, and subsequent transport processes. For example, Cd can form Cd–GSH complexes in zucchini fruit and be transported via the phloem over long distances [113]. In rice, the low-Cd line D62B exhibits significantly lower concentrations of citrate and tartrate in xylem sap compared with the high-accumulating line Luhui17, and these organic acid levels are positively correlated with Cd accumulation, indicating that organic acid composition directly influences Cd transport capacity [114]. This association suggests that organic-acid composition may contribute to genotypic differences in Cd transport capacity, although correlation alone does not establish direct causality.

Vascular transport is also influenced by the capacity of tissues to retain PTEs before they reach distal sinks [115,116]. Cell-wall binding and vacuolar sequestration can reduce the fraction available for long-distance remobilization; for example, the low-Cd Chinese cabbage cultivar LB70 retains a greater proportion of Cd in root cell-wall fractions, and phosphorus treatment can further enhance Cd retention and reduce root-to-shoot translocation [117]. At the whole-plant level, source–sink relationships further influence redistribution during reproductive development; in rice, vegetative organs can serve as Cd sources during grain filling, whereas nodes, glumes, and other tissues may act as competing sinks that influence grain Cd allocation [116]. These processes are discussed in greater detail in Section 6 as components of spatial allocation and cellular immobilization.

Overall, internal PTE transport is governed by the combined effects of vascular loading and unloading, transporter specificity, ligand-mediated mobility, and source–sink redistribution. These mechanisms do not contribute equally in all crop–element combinations, and their relative importance determines how efficiently the PTE pool entering the plant is ultimately delivered to edible organs.

Xylem loading controls root-to-shoot PTE transport, whereas phloem redistribution contributes to the delivery of mobile elements from source tissues to developing sinks (Figure 3). Transporter systems and metal-binding ligands regulate vascular loading, chemical speciation, and transport mobility, while source-sink relationships influence the final direction of redistribution.

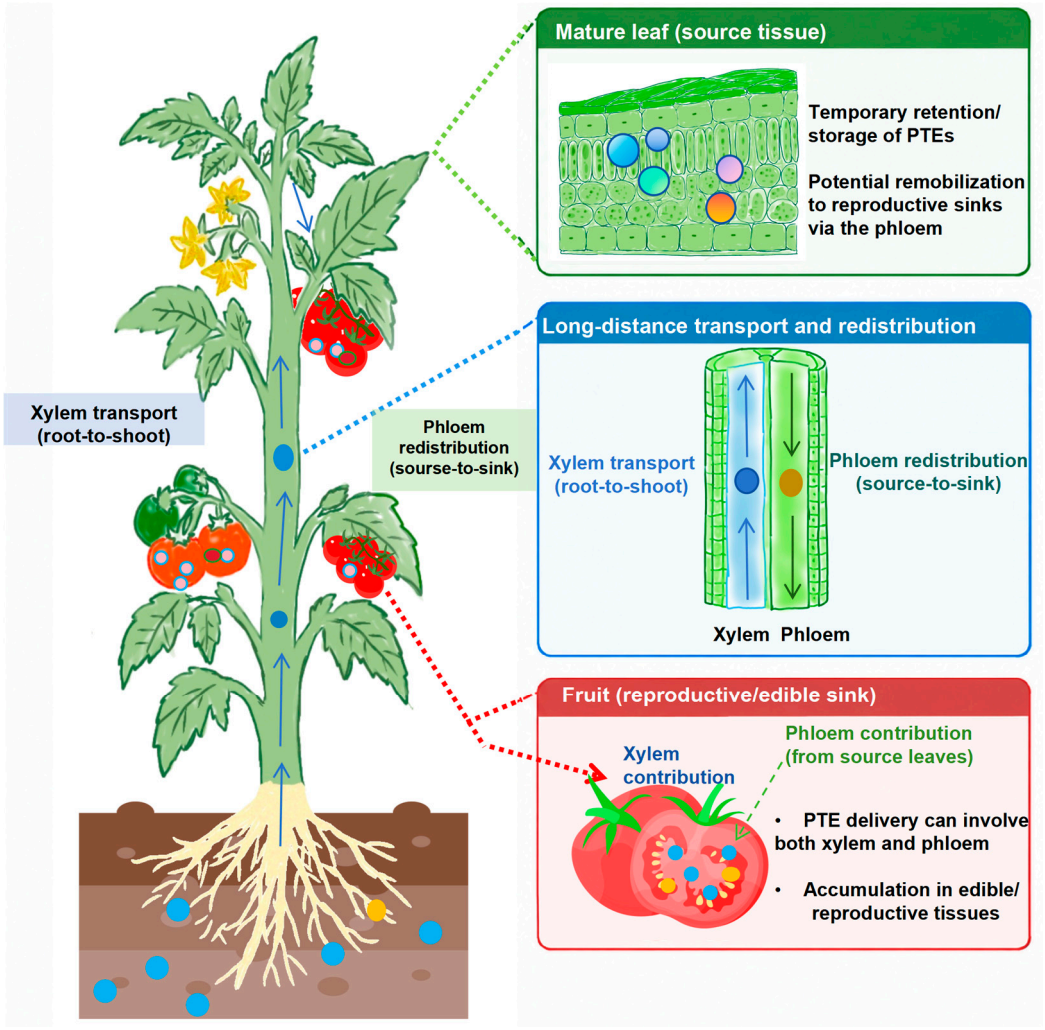


Figure 3. Regulation of PTE transport and redistribution within plants.

Representative genes involved in these and other regulatory processes, together with their functional evidence and field-validation status, are summarized in Table 2.

Xylem loading controls root-to-shoot PTE transport, whereas phloem redistribution contributes to the delivery of mobile elements from source tissues to developing sinks. Transporter systems and metal-binding ligands regulate vascular loading, chemical speciation, and transport mobility, while source–sink relationships influence the final direction of redistribution.

Table 2. Representative genes involved in the regulation of PTE accumulation and distribution in food crops.

Crop	PTE(s)	Gene/Protein	Major Molecular Function	Experimental Evidence/System	Regulatory Process in the Proposed Framework	Phenotypic Implication for PTE Accumulation	Evidence Type	Field Validation	Ref.
Rice (*Oryza sativa*)	Cd, Mn	OsNRAMP5	Major root transporter responsible for Mn and Cd uptake	Mutant lines with altered OsNRAMP5 activity; Cd accumulation and agronomic traits evaluated under controlled soil conditions	Entry restriction	Loss or modification of OsNRAMP5 strongly reduces Cd entry and lowers grain Cd accumulation, although effects on Mn nutrition indicate a potential nutrient trade-off	Genetic/ functional validation	No direct field validation reported	[28,29]
Broccoli (*Brassica oleracea* var. *italica*)	Cd	HMA4	Associated with xylem loading and root-to-shoot Cd transport	Exogenous tryptophan treatment altered HMA4 expression and shoot Cd accumulation	Transport modulation	Tryptophan treatment repressed HMA4 expression and was accompanied by a 51.6% reduction in shoot Cd accumulation	Intervention + expression association	No field validation reported	[90]
Rice (*Oryza sativa*)	Cd, Zn	OsHMA2	Mediates Zn/Cd xylem loading and root-to-shoot transport; also contributes to redistribution	Functional characterization of OsHMA2 in rice transport pathways	Transport modulation	Altered OsHMA2 activity affects Cd and Zn movement from roots toward shoots and sink tissues	Functional evidence	No direct field validation reported	[91]
Rice (*Oryza sativa*)	Cd, Zn	OsZIP7	Facilitates Zn/Cd xylem loading in roots and intervascular transfer at nodes	Functional characterization of xylem loading and node-mediated intervascular transfer	Transport modulation/spatial allocation	Regulates Zn and Cd delivery through xylem–phloem transfer and influences transport toward developing grain	Functional evidence	No direct field validation reported	[93]
Radish (*Raphanus sativus*)	Cd	RsNRAMP5	Major transporter promoting Cd influx into root cells	Functional characterization of RsNRAMP5-mediated Cd influx and accumulation	Entry restriction	RsNRAMP5 promotes root Cd uptake and accumulation, identifying it as a potential entry-control target	Functional evidence	No field validation reported	[94]

Table 2. *Cont.*

Crop	PTE(s)	Gene/Protein	Major Molecular Function	Experimental Evidence/System	Regulatory Process in the Proposed Framework	Phenotypic Implication for PTE Accumulation	Evidence Type	Field Validation	Ref.
Rice (*Oryza sativa*)	Cd	OsHMA3	Tonoplast-localized transporter mediating Cd sequestration into root vacuoles	Knockout- and overexpression-based functional validation of vacuolar Cd sequestration	Cellular immobilization	Root vacuolar sequestration reduces the mobile Cd pool and restricts Cd translocation toward shoots and grain	Genetic/ functional validation	Field-relevant evidence available from OsHMA3 overexpression studies	[118,119]
Rice (*Oryza sativa*)	Cd	OsABCC9	Tonoplast-localized ABC transporter involved in vacuolar Cd sequestration	Functional characterization of Cd tolerance and accumulation in rice	Cellular immobilization	Enhances Cd tolerance and restricts Cd movement from roots to shoots by increasing intracellular sequestration	Functional evidence	No field validation reported	[120]

Note: Evidence categories were assigned according to the nature of the supporting experiments. "Association" indicates correlations between gene expression or molecular variation and PTE accumulation without direct functional manipulation. "Intervention-based evidence" indicates that chemical or agronomic treatment altered both gene expression and PTE accumulation, but does not by itself establish a causal role for the molecular target. "Genetic/functional validation" refers to evidence from mutation, knockout, overexpression, complementation, direct transport assays, or equivalent functional characterization. Field validation was considered separately when the low-accumulation phenotype was demonstrated under agricultural field conditions. Abbreviation: PTE, potentially toxic element.

6. Regulation of Tissue Partitioning and Cellular Compartmentation

After PTEs have entered the plant and undergone long-distance transport, their final concentrations in edible organs depend on how they are partitioned among tissues and retained within specific cellular compartments. This stage therefore determines the spatial fate of PTEs after uptake and transport and represents a major control over whether absorbed PTEs ultimately reach harvested tissues.

6.1. Organ-Specific Partitioning and Spatial Allocation of PTEs

Different crop types exhibit distinct patterns of PTE partitioning among roots, vegetative tissues, and edible organs, reflecting differences in internal transport, retention, and source–sink relationships. Importantly, low PTE concentrations in edible tissues can result from preferential allocation to non-edible organs even when total plant uptake is not particularly low. PTE accumulation in edible organs varies considerably among crop species and harvested tissue types. Comparative evidence indicates that cole crops and water spinach can accumulate substantially more Cd than garlic, onion, and pea, reflecting species-specific differences in Cd chemical forms and transport capacity [31,121]. These observations highlight the importance of crop identity and internal Cd partitioning when evaluating low-accumulation potential. Importantly, tissue partitioning is also strongly element-dependent. Cd is generally more mobile within plants and can be redistributed toward grains or fruits, whereas Pb is often more strongly retained in roots and other non-edible tissues. The distribution of As is additionally influenced by its chemical speciation and the transport pathways used by different As species, while crop-specific evidence for Hg partitioning remains comparatively limited [20,21,27]. Therefore, organ-specific accumulation patterns identified for one PTE should not be directly generalized to another.

Leaves serve as both transpiring organs and edible tissues in leafy vegetables, making them important destinations for PTEs transported from roots. Comparative analyses have revealed higher Cd accumulation and root-to-shoot transport capacity in water spinach than in garlic, partly associated with differences in the chemical fractions of Cd within plant tissues [121]. Furthermore, comparisons among spinach, kale, and amaranth demonstrate that the efficiency of Cd translocation varies substantially among leafy vegetables [122]. These observations indicate that edible-leaf accumulation reflects not only root uptake but also the efficiency of root-to-shoot transport and subsequent retention within leaf tissues.

In radish (*Raphanus sativus* L.), substantial genotypic variation in Cd accumulation has been reported, supporting the identification of low-Cd cultivars [123]. Further comparative evidence indicates that radish cultivars differ in Cd absorption, root-to-shoot translocation, subcellular distribution, and chemical forms, highlighting the contribution of genotype-dependent transport and partitioning processes [124]. In potato, Cd shows even stronger compartmentalization, with the majority retained in leaves and stems, and only a small fraction transported to tubers [125]. These examples demonstrate that the concentration measured in an edible belowground organ cannot be inferred directly from total root accumulation because metals may be unevenly distributed among epidermal, storage, and other root-derived tissues.

Fruit-bearing vegetables and fruit trees often exhibit comparatively restricted PTE transfer to harvested fruits. In tomato, cucumber, and pepper, substantial proportions of Cd and Pb may be retained in roots or vegetative tissues, resulting in lower concentrations in fruits [32,126]. Fruit-bearing crops may restrict Cd transfer to harvested fruits through tissue-specific retention and transport regulation. In fruit trees such as apple, a substantial fraction of accumulated PTEs may remain in vegetative organs rather than being transferred to fruits [14,127]. In tomato and eggplant, grafting combined with exogenous selenium

application has been shown to reduce Cd accumulation in fruits, demonstrating that organ-specific allocation can also be modified through appropriate agronomic interventions [128].

Cereal crops also show clear organ-specific partitioning patterns, often characterized by preferential retention in vegetative tissues. In rice, Cd is mainly accumulated in roots and straw, with only a fraction transported to grains [23]. In wheat, Cd is primarily enriched in roots and stems [129,130], whereas in maize, Cd and Pb are largely retained in roots and vegetative organs [131]. In rice, nodes function as important regulatory barriers controlling Cd delivery to grains. Recent evidence indicates that genotype-dependent differences in cell-wall pectin enrichment and amino-acid-mediated chelation contribute to Cd retention within nodes, thereby limiting its subsequent transfer to grains [132]. This demonstrates that low grain Cd accumulation may arise from restricted transport at intermediate vascular checkpoints rather than from reduced root uptake alone. However, substantial genotypic variation can occur within the same crop species. For instance, soybean cultivars show distinct "root-retention" and "grain-accumulation" strategies, with grain Cd concentrations positively correlated with concentrations in vegetative tissues [133]. In durum wheat, Cd partitioning and accumulation change dynamically during grain filling, and comparisons between near-isogenic lines further indicate that genotype can influence the distribution of Cd among plant compartments during reproductive development [134]. Thus, organ-specific PTE allocation is dynamic rather than fixed and can change during development as source–sink relationships shift.

Taken together, PTE partitioning among plant organs is shaped by crop type, genotype, element identity, and developmental stage. Preferential retention in roots or vegetative tissues can reduce PTE delivery to edible organs, whereas remobilization toward reproductive sinks can increase grain or fruit accumulation later in development. Spatial allocation should therefore be viewed as a dynamic control process rather than a fixed tissue-distribution pattern.

6.2. Cell-Wall Immobilization and Vacuolar Sequestration

At the cellular scale, PTE mobility is regulated by extracellular cell-wall immobilization and intracellular vacuolar sequestration, but their contributions to reducing long-distance transport depend on the tissues in which metals are retained. In pak choi, exogenous glutathione enhanced phytochelatin synthesis and the expression of BcABCC1 and BcABCC2, promoting Cd sequestration in root vacuoles and reducing its subsequent translocation to edible shoots [135]. Similarly, comparative analyses of tobacco cultivars revealed that stronger root cell-wall binding and vacuolar sequestration were associated with lower Cd translocation to leaves, whereas cultivars with weaker root retention exhibited greater Cd transfer to aerial tissues and enhanced glandular-trichome secretion [136]. Together, these findings highlight that the spatial location of metal immobilization is critical for determining whether cellular detoxification contributes to reduced PTE accumulation in harvested tissues.

The cell wall constitutes an important apoplastic barrier and extracellular binding matrix for PTEs. It is enriched in pectin, cellulose, and hemicellulose, whose functional groups (e.g., carboxyl and hydroxyl groups) provide abundant binding sites for metal ions such as Cd and Pb, thereby immobilizing them in the apoplastic space [137]. Root cell walls constitute important sites for Cd retention and can restrict its subsequent entry into long-distance transport pathways. In rice, Fe supplementation enhanced Cd retention through iron-plaque formation and root cell-wall binding, thereby reducing Cd mobility in the xylem. Under the reported experimental conditions, grain Cd concentration decreased from 0.44 to 0.20 mg kg^{-1} following Fe fertilization [138]. These findings illustrate how nutrient management can influence cell-wall immobilization and ultimately reduce Cd

delivery to edible grains. In tomato, Cd stress significantly enhances the accumulation of cell wall polysaccharides, thereby increasing Cd adsorption capacity [139]. Similarly, low-Cd pak choi varieties exhibit stronger Cd-binding capacity in the cell wall due to a higher pectin content and reduced pectin methyl esterification, which enhances metal immobilization efficiency [140]. These findings support cell-wall retention as an important mechanism limiting the fraction of Cd available for entry into the symplast and subsequent long-distance transport.

Vacuolar sequestration provides an intracellular mechanism for reducing the mobile pool of PTEs. Tonoplast-localized transporters, including HMA3 and members of the ABCC family, participate in the compartmentalization of metal ions or their complexes [141,142]. In rice, targeted expression of OsHMA3 driven by the OsYSL16 promoter reduced Cd transport toward aerial tissues and decreased grain Cd concentrations by more than 70% [141]. These findings provide genetic evidence that enhancing appropriate tissue-specific Cd sequestration can be an effective strategy for developing low-Cd crops. For example, rice OsHMA3 mediates Cd sequestration into root vacuoles, significantly reducing Cd translocation to shoots and grains [118]. In *Brassica rapa* vegetables, BrHMA3-dependent vacuolar compartmentation effectively decreases Cd accumulation in edible tissues [143]. In addition, OsABCC9 is induced under Cd stress and contributes to vacuolar Cd sequestration, thereby enhancing tolerance and restricting Cd transport to shoots [120]. Unlike cell-wall binding, which operates in the apoplast, vacuolar sequestration acts after PTEs have entered the symplast and therefore represents a distinct intracellular control mechanism.

Cell-wall immobilization and vacuolar sequestration can act as complementary mechanisms that reduce the mobile PTE pool at different cellular locations. Cell wall binding reduces the fraction of metals entering the symplastic pathway, whereas vacuolar sequestration further decreases the pool of free cytosolic metals, thereby limiting their availability for long-distance transport. For instance, in rapeseed, potassium application enhances lignin and cellulose deposition in cell walls, promoting root retention of Cd and reducing its translocation factor [144]. In tobacco, Cd translocation factors vary widely (0.12–1.51), with low-translocation varieties exhibiting stronger capacities for both cell wall binding and vacuolar sequestration [136]. Moreover, in soybean, GA treatment can mitigate Ni stress partly by modulating cell-wall fixation, indicating that cellular immobilization responses are not restricted to Cd [145].

Together, cell-wall retention and vacuolar sequestration reduce the fraction of PTEs available for long-distance redistribution, but they operate through spatially distinct mechanisms: one in the apoplast and the other within intracellular compartments. Their contribution to low-accumulation phenotypes therefore depends on the tissue in which immobilization occurs and on whether retention prevents subsequent transfer toward edible organs.

Overall, spatial allocation and cellular immobilization determine where PTEs are retained after entry and long-distance transport (Figure 4). A low-accumulation phenotype may therefore arise not only from reduced PTE uptake or transport, but also from preferential retention in non-edible organs and reduced remobilization toward harvested tissues. Importantly, the effectiveness of these mechanisms for food-safety-oriented crop improvement depends on the location of retention: immobilization in roots or non-edible tissues can directly restrict PTE delivery to edible organs, whereas sequestration within edible tissues may enhance tolerance without necessarily reducing contaminant concentrations in the harvested product.

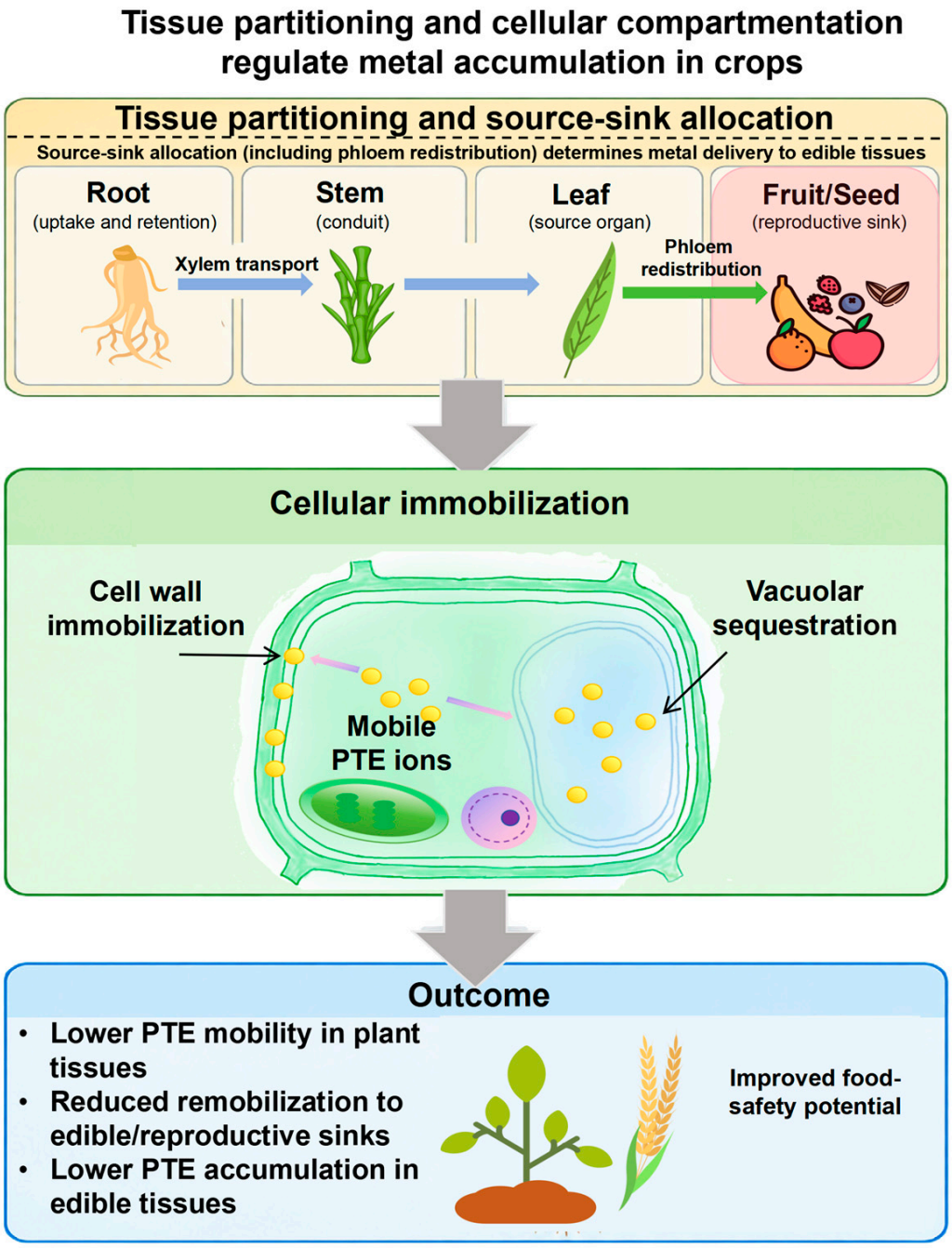


Figure 4. Spatial allocation and cellular immobilization of PTEs within crops.

Illustrative quantitative and comparative evidence supporting different low-accumulation mechanisms is summarized in Table 3. The table distinguishes direct reductions in harvested edible organs from changes measured only in roots or vegetative shoots, because these outcomes differ substantially in their relevance to food safety.

At the whole-plant level, preferential retention in roots or vegetative tissues and source–sink relationships regulate the allocation of PTEs toward edible organs. At the cellular level, cell-wall binding retains PTEs in the apoplast, whereas vacuolar sequestration reduces the mobile cytosolic PTE pool. These processes can restrict subsequent remobilization and delivery to harvested tissues, although their effectiveness depends on crop genotype, element identity, developmental stage, and the tissue in which immobilization occurs.

Table 3. Illustrative quantitative and comparative evidence for mechanisms reducing PTE accumulation in food crops.

Crop	PTE(s)	Experimental Context	Major Regulatory Mechanism	Reported Effect on PTE Accumulation	Outcome Relevance	Agronomic/Nutritional Consequence	Evidence Level and Validation	Ref.
Water spinach (*Ipomoea aquatica*)	Cd, Pb	Controlled bacterial-inoculation study; immobilization assays included 10 mg L^{-1} Cd and 20 mg L^{-1} Pb	Entry restriction: polyamine-mediated chelation, cell-surface adsorption and precipitation reduced rhizosphere metal availability	Cd and Pb concentrations in edible shoots were 51–80% lower than in non-inoculated controls; acid-soluble Cd and Pb fractions in the rhizosphere were also reduced	Direct edible-tissue evidence	Plant-growth-promoting effects were reported, although yield-scale validation was not performed	Intervention-based; controlled experiment	Wang et al., 2022 [69]
Broccoli (*Brassica oleracea* var. *italica*)	Cd	Growth-chamber pot experiment; 0–30 mg kg^{-1} Cd in substrate, with or without 15 mg kg^{-1} tryptophan	Transport modulation: reduced root-to-shoot transport, associated with repression of HMA4 and reduced xylem loading	Shoot Cd concentration decreased by 51.6% relative to Cd treatment alone	Indirect shoot evidence	Shoot and root fresh weights increased by approximately 25% and 120%, respectively, relative to Cd treatment alone	Intervention + transcriptomic evidence; controlled experiment	Jiang et al., 2022 [90]
Wheat (*Triticum aestivum*)	Cd	Seedling experiment; 10 μM Cd with 1 mM Si	Entry/transport modulation: Si-mediated regulation of Lsi-, ZIP-, NRAMP5- and HIPP-related pathways and ionic homeostasis	Cd concentration decreased by 67.45% in roots and 70.34% in shoots	Indirect root/shoot evidence	Si alleviated growth and photosynthetic inhibition and improved ionic/redox homeostasis; grain Cd was not evaluated	Intervention + transcriptomic evidence; controlled experiment	Liu et al., 2023 [95]
Rice (*Oryza sativa*)	Cd	CRISPR/Cas9-derived OsNramp5 mutants grown in soils amended with 1 or 5 mg kg^{-1} Cd	Entry restriction: reduced OsNRAMP5-mediated root Cd uptake	At 1 mg kg^{-1} soil Cd, grain Cd decreased by 95–97% among three mutants (0.016–0.032 vs. 0.659 mg kg^{-1} in WT)	Direct grain evidence	Grain Mn decreased, whereas Fe and Zn were largely unchanged; yield penalties occurred and depended on mutation severity, illustrating an important Cd–Mn trade-off	Genetic/functional evidence; controlled pot validation	Wang et al., 2019 [28]

Table 3. *Cont.*

Crop	PTE(s)	Experimental Context	Major Regulatory Mechanism	Reported Effect on PTE Accumulation	Outcome Relevance	Agronomic/Nutritional Consequence	Evidence Level and Validation	Ref.
Rice (*Oryza sativa*, *indica*)	Cd	Elite cultivar overexpressing OsHMA3, tested in two Cd-contaminated paddy soils; agronomic traits assessed under field-relevant conditions	Cellular immobilization: enhanced root vacuolar sequestration limits root-to-shoot Cd translocation	Brown-rice Cd decreased by 94–98%, reaching approximately 0.01–0.04 mg kg^{-1}	Direct grain evidence	No significant effect on grain yield or grain Zn, Fe, Cu and Mn concentrations in field trials	Genetic/functional + field-relevant validation	Lu et al., 2019 [119]
Maize (*Zea mays*)	Cd	Field screening of 95 genotypes followed by hydroponic comparison of low-Cd L63 and high-Cd L42; mechanistic tests included 5 μM Cd	Transport modulation: stronger root retention and lower xylem-loading/root-to-shoot transport in L63	L63 showed significantly lower grain and shoot Cd than L42; percentage reduction was not reported in the current synthesis	Direct grain + supporting shoot evidence	L63 showed less Cd-induced growth inhibition than L42	Comparative genotype evidence + field and hydroponic validation	Lin et al., 2022 [87]
Pak choi (*Brassica chinensis*)	Cd	Comparison of low- and high-Cd-accumulating cultivars	Spatial allocation/cellular immobilization: stronger root cell-wall retention and vacuolar sequestration in low-Cd cultivars	Low-Cd cultivars showed lower leaf and stem Cd concentrations and stronger root retention than high-Cd cultivars; a directly comparable percentage reduction was not available for inclusion in this synthesis	Direct edible-shoot evidence	Low-Cd cultivars showed distinct detoxification requirements; agronomic yield effects were not reported	Comparative physiological evidence; controlled experiment	Xue et al., 2014 [86]

Table 3. *Cont.*

Crop	PTE(s)	Experimental Context	Major Regulatory Mechanism	Reported Effect on PTE Accumulation	Outcome Relevance	Agronomic/Nutritional Consequence	Evidence Level and Validation	Ref.
Tomato (*Solanum lycopersicum*)	Cd	GWAS of 506 accessions plus genetic and grafting validation; controlled mild-Cd treatment (1 mg kg^{-1} Cd, 30 d)	Entry/transport regulation: natural LCT1 allele reduces Cd accumulation primarily through root-dependent regulation	The low-Cd allele was associated with reduced Cd in shoots and fruits; proportion of low-Cd accessions increased from 32.40% to 64.96% during improvement from CER to large-fruited cultivated tomato	Direct fruit evidence	Low-Cd LCT1□ was co-selected with the large-fruit fw3.2□ allele, providing evidence that low Cd and high-yield/large-fruit traits can coexist	Association + genetic/grafting validation; controlled greenhouse study	Zhang et al., 2025 [30]

Note: Studies were selected as illustrative examples when they investigated food crops, addressed at least one of the four regulatory processes proposed in this review, and provided quantitative or clearly comparative evidence for differences in PTE accumulation. Priority was given to studies reporting PTE concentrations in edible organs, agronomic or nutritional consequences, and/or field-relevant validation. Studies reporting only root or vegetative-shoot responses were retained when they provided mechanistic evidence relevant to entry restriction or transport regulation. "Direct edible-organ evidence" refers to measurements obtained from harvested edible tissues such as grain, fruit, or edible shoots, whereas "indirect root/shoot evidence" refers to changes measured only in non-harvested roots or vegetative tissues. Reported percentage changes refer to the specific tissue, treatment, and experimental endpoint used in the original study and should not be interpreted as directly comparable effect sizes across studies. Evidence categories distinguish comparative/associative observations, experimental interventions, genetic or functional validation, and field-relevant validation. Abbreviations: PTE, potentially toxic element; NR, not reported.

7. Screening, Improvement, and Field Deployment of Low-Accumulation Crops

Representative quantitative and comparative evidence supporting different low-accumulation mechanisms is summarized in Table 3. Importantly, the magnitude and agronomic relevance of reported effects vary substantially with crop species, target element, experimental system, and the tissue used for evaluation.

7.1. Evaluation and Identification of Low-Accumulation Crops

The accurate identification of low-accumulation crops requires an evaluation framework centered on PTE concentrations in edible tissues rather than on whole-plant accumulation alone. Because crop species differ substantially in edible organs and internal PTE partitioning, indices such as the bioaccumulation factor (BCF) and translocation factor (TF) cannot by themselves indicate whether a harvested product is suitable for food use. The evaluation of low-accumulation crops should prioritize PTE concentrations in edible tissues and their compliance with applicable commodity- and element-specific food-safety standards. Bioaccumulation factors and translocation factors provide useful supplementary information but cannot independently establish whether a harvested product is suitable for consumption [146]. For example, a three-year, three-site field investigation involving 55 rice varieties identified cultivars with relatively stable low Cd and Hg accumulation and estimated soil concentration thresholds associated with safe rice production under the investigated regional conditions [147]. This illustrates the importance of integrating edible-tissue measurements, genotype stability, and site-specific soil conditions into the screening process. However, regulatory compliance alone should not be equated with negligible dietary risk. Where food-safety relevance is being evaluated, edible-tissue concentrations should be interpreted together with consumption patterns and, when appropriate, exposure-based indicators such as estimated daily intake (EDI), hazard quotient (HQ), or hazard index (HI).

On this basis, identification should proceed from phenotypic screening to multi-environment validation and, where necessary, mechanistic characterization. Initial field or controlled-environment experiments can be used to identify candidate germplasm with consistently low PTE concentrations in edible tissues. Candidate lines should then be evaluated across contrasting soils, contamination levels, climatic conditions, and management regimes to determine whether the phenotype is stable rather than environment-specific. Molecular and genetic analyses can subsequently be used to identify the mechanisms underlying stable low accumulation and to connect phenotype with genotype. Importantly, candidate cultivars should be evaluated simultaneously for yield, essential mineral composition, and major quality traits. A genotype that reduces Cd accumulation but compromises Fe, Zn, Mn nutrition or agronomic performance should not automatically be considered an optimal low-accumulation resource.

Low-accumulation status should therefore be defined for a specific crop, edible organ, and target element rather than treated as a universal property of a cultivar. A genotype classified as low-Cd, for example, cannot be assumed to exhibit similarly low accumulation of Pb, As, or Hg without direct evaluation.

7.2. Genetic Improvement of Low-Accumulation Crops

Breeding represents an important strategy for developing crop varieties with reduced PTE accumulation in edible tissues. Traditional breeding exploits natural genetic variation and germplasm selection, whereas molecular breeding enables more targeted improvement based on mechanisms controlling PTE entry, transport, spatial allocation, and cellular immobilization [148,149]. The most useful breeding targets are therefore not necessarily

those that minimize total PTE uptake, but those that selectively reduce delivery to edible organs while maintaining mineral nutrition, yield, and crop performance.

With advances in molecular mechanisms, breeding strategies are shifting from phenotype-based selection toward mechanism-driven design. For instance, modification of OsNRAMP5-mediated Cd uptake or OsHMA3-mediated vacuolar sequestration can substantially reduce Cd accumulation in rice grain [28,29,119]. These two examples also illustrate distinct breeding routes within the framework proposed in this review: reducing PTE entry and enhancing retention in non-edible root tissues.

A major challenge, however, is that many transporters associated with toxic-element accumulation also participate in essential mineral nutrition. Members of the NRAMP, ZIP, and HMA families can transport or regulate both toxic and essential elements; consequently, modifying these pathways may alter Fe, Zn, Mn, or other micronutrient concentrations in addition to reducing PTE accumulation [20,21,27]. Breeding targets should therefore be evaluated for selectivity and pleiotropic effects rather than judged solely by the magnitude of contaminant reduction.

Genome-wide association studies (GWASs) have facilitated the identification of loci associated with low-accumulation traits and the development of markers for marker-assisted selection. For example, KASP markers derived from Cd-associated loci have enabled efficient screening of low-Cd wheat germplasm [150]. CRISPR/Cas-based gene editing also provides a tool for modifying candidate regulatory genes [151]. Nevertheless, association signals or controlled-environment phenotypes require functional and field validation before they can be regarded as reliable breeding targets.

Thus, genetic improvement should aim for a combined phenotype of low edible-tissue PTE accumulation, preserved essential mineral composition, acceptable yield, and stability across environments.

7.3. Agronomic and Soil Management Strategies

The effectiveness of low-accumulation crops is strongly influenced by soil conditions and agronomic practices [152]. Management intensity should therefore be determined not only by total soil PTE concentration but also by element identity, bioavailable fraction, soil physicochemical properties, crop species, and the applicable food-safety threshold. Low-accumulation varieties should be viewed as one component of an integrated risk-management strategy rather than as a substitute for soil remediation under all contamination scenarios.

Under relatively low-contamination or low-bioavailability conditions, low-accumulation varieties combined with appropriate agronomic management may be sufficient to maintain edible-tissue concentrations below regulatory limits. For example, low-Cd rice varieties have maintained grain Cd concentrations below relevant thresholds under mildly contaminated conditions [153]. Irrigation management and applications of silicon or phosphorus have also been reported to reduce PTE availability or crop accumulation under specific conditions [154–156]. However, such effects are element-specific and should not be generalized across PTEs; for example, management practices affecting Cd availability may influence As differently because of contrasting redox and speciation controls.

Where soil PTE availability is high or strongly variable, varietal selection alone may not provide sufficient protection against contaminant accumulation in edible organs [152]. Multi-year field evidence from rice–wheat rotation systems demonstrates that $CaCO_3$–based soil amendments can achieve sustained reductions in grain Cd concentrations, with performance influenced by amendment composition and soil conditions [157]. These findings support the integration of soil management with genetic strategies while emphasizing that the effectiveness of individual interventions must be verified under relevant field

conditions. In two-year, multi-site field trials involving rice cultivars with contrasting Cd-accumulation phenotypes, Mn-loaded biochar and limestone amendments reduced grain Cd accumulation, although the magnitude depended on soil conditions and interactions among amendments [158]. The effectiveness of these amendments should be evaluated for the specific target element and soil because an amendment that immobilizes one PTE may have little effect, or potentially a contrasting effect, on another.

Under severe contamination, the suitability of continued food-crop production should be evaluated cautiously. Integrated strategies combining soil remediation, cropping system adjustment, rotation, and low-accumulation varieties are necessary to ensure safe agricultural production [159,160]. Low-accumulation cultivars alone should not be assumed to guarantee regulatory compliance or acceptable dietary risk. In some situations, alternative land-use or non-food production strategies may be more appropriate than continued cultivation of food crops.

7.4. Genotype × Environment × Management Integration and Field Validation

Overall, the deployment of low-accumulation crops should be understood within a genotype × environment × management (G × E × M) framework. Genotype determines the intrinsic capacity for PTE entry, transport, allocation, and immobilization; environmental conditions regulate PTE speciation and bioavailability; and management practices modify both soil exposure and plant physiological responses. Consequently, a low-accumulation phenotype is not an invariant property of a genotype but the outcome of interactions among genetic background, element chemistry, soil conditions, and management.

Field validation should therefore extend beyond a single location or season. Candidate cultivars should be tested across contrasting soil types, contamination levels, climatic conditions, and management regimes, with simultaneous measurement of edible-tissue PTE concentration, yield, and essential nutrient composition. Multi-location and multi-season testing is particularly important for distinguishing robust low-accumulation traits from phenotypes that are specific to controlled environments or individual sites.

The ultimate criterion for deployment should be reliable reduction in PTE concentrations in harvested tissues under realistic production conditions without unacceptable penalties in yield or nutritional quality. Where relevant, regulatory compliance should be complemented by dietary-exposure assessment. Thus, successful field deployment requires convergence of three outcomes: stable low accumulation, acceptable agronomic and nutritional performance, and demonstrable food-safety benefit.

8. Integrated Discussion: From Mechanistic Evidence to Field-Relevant Low-Accumulation Phenotypes

8.1. Different Regulatory Routes Can Converge on Similar Low-Accumulation Phenotypes

The evidence synthesized in this review supports the view that low accumulation in edible tissues is an emergent phenotype rather than the consequence of a universally dominant mechanism. Across crop–element systems, different combinations of entry restriction, transport modulation, spatial allocation, and cellular immobilization can produce comparable reductions in edible-tissue PTE concentrations. This mechanistic heterogeneity explains why root accumulation alone is often insufficient to classify low-accumulation germplasm and highlights the need to identify the dominant control process underlying each phenotype.

8.2. Element Specificity and Uneven Evidence Across Crop–PTE Systems

The relative importance of individual regulatory processes is strongly element-dependent. For cationic PTEs such as Cd, soil pH, cation competition, transporter specificity,

and root-to-shoot transport can strongly influence accumulation. In contrast, As behavior is strongly influenced by chemical speciation, redox conditions, Fe mineral dynamics, and the transport pathways used by different As species [27,161]. Pb is generally less mobile within plants and is often more strongly retained in roots and other vegetative tissues, whereas mechanistic evidence for Hg accumulation and internal redistribution in food crops remains comparatively limited.

These differences mean that mechanisms established for one element should not be assumed to operate with the same relative importance for another. In particular, the current evidence base is strongly weighted toward Cd, with rice representing one of the most intensively investigated crop systems. Evidence for Pb, As, Hg, and many non-rice crop–element combinations is less extensive and often less mechanistically resolved. This imbalance reflects the current distribution of available research rather than equivalent support across all PTEs and crop groups.

Accordingly, the four-process framework proposed here is intended to provide a common analytical structure for comparing entry restriction, transport modulation, spatial allocation, and cellular immobilization across crop–element systems, and not to imply that the same molecular mechanisms dominate in each case. Cross-element generalization should therefore be made at the level of regulatory processes, whereas specific transporters, chemical controls, tissue-partitioning patterns, and immobilization mechanisms require direct validation for each crop–PTE combination.

8.3. Evidence Strength and Agronomic Trade-Offs

The strength of evidence supporting proposed low-accumulation mechanisms varies substantially. Associations between transporter expression, root traits, or metabolite abundance and PTE concentration provide mechanistic clues but do not establish causality. Likewise, short-term nutrient, amendment, or chemical treatments that simultaneously alter gene expression and PTE accumulation provide intervention-based evidence but do not necessarily demonstrate that the associated molecular target is directly responsible for the observed phenotype.

In this review, evidence is therefore interpreted according to the nature of the supporting experiments rather than through a formal risk-of-bias score. Associative observations are distinguished from intervention-based evidence, genetic or functional validation, and field-relevant validation. Genetic modification, mutation, knockout, overexpression, complementation, direct transport assays, or equivalent functional experiments provide stronger support for a causal role, whereas field validation addresses a different question: whether the low-accumulation phenotype remains effective under agronomically realistic conditions. A mechanism supported by genetic or functional evidence may therefore still require independent evaluation of environmental stability and field performance.

Mechanistic strength alone is also insufficient for identifying desirable breeding or management targets. Many transport pathways involved in PTE uptake and redistribution also contribute to the acquisition or homeostasis of essential nutrients. For example, transporters involved in Cd movement may also influence Mn, Zn, or Fe nutrition [20,21,27]. Consequently, a large reduction in PTE accumulation should not automatically be interpreted as an agronomic improvement if it is accompanied by impaired mineral nutrition, reduced biomass, lower yield, or unstable performance across environments.

Accordingly, promising low-accumulation mechanisms should be evaluated across at least four dimensions: mechanistic support, reduction in PTE concentrations in edible tissues, effects on essential mineral nutrition and crop productivity, and robustness under field conditions. Mechanisms supported across these dimensions are more relevant

for breeding and agronomic deployment than those demonstrated only under a single controlled experimental condition.

8.4. Low Accumulation Is Not Equivalent to Low Dietary Risk

Reduced PTE concentrations in edible tissues are a prerequisite for safer food production, but they do not by themselves demonstrate negligible dietary risk [162]. Regulatory compliance is generally determined by comparing contaminant concentrations with commodity- and element-specific maximum limits, whereas dietary exposure additionally depends on food-consumption rate, exposure frequency, body weight, and population-specific dietary patterns [163–165].

Accordingly, evaluation of low-accumulation crops should distinguish concentration-based compliance from exposure-based health risk. Where sufficient information is available, edible-tissue PTE concentrations can be complemented by indicators such as estimated daily intake (EDI), hazard quotient (HQ), hazard index (HI), and carcinogenic risk. This distinction is particularly important for staple foods or vegetables consumed in large quantities for which moderate contaminant concentrations may still contribute substantially to long-term dietary exposure [162–165].

Low-accumulation strategies should therefore be evaluated not only by the magnitude of contaminant reduction in harvested tissues, but also by whether that reduction meaningfully decreases dietary exposure while maintaining agronomic and nutritional performance.

8.5. Toward Predictive Validation of Low-Accumulation Phenotypes

Future studies should evaluate multiple regulatory processes within the same crop–element–environment system rather than examining individual mechanisms in isolation. Simultaneous measurements of root entry, vascular transport, organ-specific allocation, cellular immobilization, and PTE concentrations in harvested tissues would allow the relative contribution of different control processes to be compared within a common experimental framework. These measurements should be integrated with agronomic endpoints, including yield, essential mineral composition, and relevant food-safety indicators.

Multi-genotype and multi-environment experiments will be particularly important for determining whether the dominant control point underlying a low-accumulation phenotype is stable or shifts with soil properties, contamination level, climate, developmental stage, or management practice. A mechanism that dominates under one experimental condition may contribute less under another, and apparent genotype differences may therefore reflect both intrinsic regulatory traits and genotype–environment interactions.

9. Conclusions and Perspectives

Low accumulation of PTEs in crops is an emergent phenotype generated by multiple regulatory processes across the soil–plant continuum. Entry restriction, transport modulation, spatial allocation, and cellular immobilization represent distinct but interacting control processes whose relative contributions vary among elements, crop species, genotypes, and environments. Similar low-accumulation phenotypes may therefore arise through different mechanistic routes rather than through a single universal pathway.

Future research should move beyond documenting reduced accumulation toward identifying the dominant control processes underlying individual low-accumulation phenotypes. Greater emphasis is needed on cross-element comparisons, functional validation, mixed-contamination scenarios, nutrient and yield trade-offs, and multi-location and multi-season field testing. Mechanistic targets should be prioritized only when reductions in edible-tissue PTE concentrations are accompanied by acceptable mineral nutrition, crop productivity, and environmental stability.

Ultimately, the practical value of low-accumulation crops should be assessed using an integrated endpoint combining stable reductions in edible-tissue PTE concentrations, maintenance of yield and essential nutrient quality, field robustness, and demonstrable food-safety benefit. Integrating mechanistic understanding with genotype selection and environment-specific management may provide a practical basis for reducing dietary PTE exposure while maintaining agricultural productivity.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy16212224/s1, Table S1: Thematic search strategies used for literature identification in the Web of Science Core Collection.

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